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Abstract: Understanding how species diversity affects plant performance is a central question in biodiversity–ecosystem functioning (BEF) research. At the community level, functional trait means and trait dissimilarities have been used to explain biodiversity effects, but with mixed success. To disentangle how functional traits explain community growth and underpin biodiversity–ecosystem functioning relationships, we should elucidate how plant traits affect individual growth across species richness levels, because the role of functional traits on growth depends on the ecological context of the individual. We addressed this topic by using detailed data of twelve functional traits and annual growth for 529 individual trees of 31 species at five species-richness levels in a large forest biodiversity experiment in south-east China from 4 to 9 years after planting. Our analyses show first that individual trait values can change with species richness, indicating that trait values can change due to the biotic context. Secondly, we show that early tree growth is more strongly affected by traits than by species richness. Finally, our data show that growth–trait relationships can change with species richness and with forest age. Trait effects on growth are more pronounced at higher richness levels, indicating that measuring traits on individual trees across richness levels can improve growth predictions and inference of BEF relationships that are shaped by functional traits. Synthesis. This study shows that functional trait values and their effect on individual tree growth depend on species richness. Our data support the notion that to elucidate how functional traits shape biodiversity–ecosystem functioning relationships, an important step is to consider the biotic context of individual trees within a community. We have made an initial step by analysing how functional traits affect individual-tree growth in a diversity-dependent manner and future research should continue by elucidating the role of traits on tree–tree interactions across diversity levels.

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Abstract

1. Understanding how species diversity affects plant performance is a central question in biodiversity–ecosystem functioning (BEF) research. At the community level, functional trait means and trait dissimilarities have been used to explain biodiversity effects, but with mixed success. We argue that to disentangle how functional traits explain community growth and underpin biodiversity–ecosystem functioning relationships, we should elucidate how plant traits affect individual growth across species richness levels, because the role of functional traits on growth depends on the ecological context of the individual.
2. We addressed this topic using detailed data of twelve functional traits and annual growth for 529 individual trees of 31 species at five species-richness levels in a large forest biodiversity experiment in south-east China from 4–9 years after planting.
3. Our analyses show first that individual trait values can change with species richness, indicating that trait values can change due to the biotic context. Secondly, we show that early tree growth is more strongly affected by traits than by species richness. Finally, our data show that growth–trait relationships can change with species richness and with forest age. The trait effects on growth are more pronounced at higher richness levels, indicating that measuring traits on individual trees across richness levels can improve growth predictions and inference of BEF relationships that are shaped by functional traits.
4. *Synthesis*. This study shows that functional trait values and their effect on individual tree growth depend on species richness level. Our data support the notion that to elucidate how functional traits shape biodiversity–ecosystem functioning relationships, an

important step is to consider the biotic context of individual trees within a community. We have made an initial step by analyzing how functional traits affect individual-tree growth in a diversity-dependent manner and future research should continue by elucidating the role of traits on tree–tree interactions across diversity levels.

Key words: BEF-China, ecosystem function, plant development and life-history traits, individual growth, species diversity, trait variation, tree growth

INTRODUCTION

How species richness affects plant performance is a central question in community ecology and especially in biodiversity–ecosystem functioning (BEF) research. In most BEF-related studies a positive relationship between species richness and community performance has been observed (Balvanera et al., 2006; Liang et al., 2016; Weisser et al., 2017; Huang et al., 2018). However, the effect of species richness on the relationship between plant traits and performance has often been ignored. This lack of individual-level studies in BEF research is a drawback because interactions between individual trees and with the environment are driving growth and performance of individuals, which then scale up to community-level biodiversity effects (Fichtner et al., 2018; Yang, Cao & Swenson, 2018). Important aspects of these interactions between individuals are functional traits that underlie performance through resource competition and facilitation. Functional traits are typically defined as morphological or physiological characteristics that determine the growth and performance of an individual within an environmental context. Because traits can change plastically in response to environmental conditions (Roscher, Schmid, Buchmann, Weigelt & Schulze, 2011; Lipowsky et al., 2015), and the composition and richness of species can affect the local environmental conditions, it is expected that trait effects on individual tree growth will also depend on the species richness at community or local neighbourhood level.

Functional traits have been used to describe the broad variation of plants all over the globe and define plant ecological strategies, from fast (acquisitive) to slow (conservative)-growing species (Wright et al., 2004; Reich, 2014; Díaz et al., 2016). Traits that are linked to resource capture (e.g. branch number and leaf area) and photosynthetic capacity (e.g.

specific leaf area and leaf nitrogen content) or nutrient and water uptake (e.g. specific root length and root diameter) generally have positive relationships with growth (Poorter & Bongers, 2006; Comas & Eissenstat, 2012). In turn, traits that are related to structural and hydraulic safety (e.g. wood density) or longevity (e.g. leaf dry-matter content and leaf/root density) have negative relationships with growth but are often positively related to survival (Poorter & Bongers, 2006; Chave et al., 2009). However, inconsistencies are observed for these growth–trait relationships (Poorter et al., 2008; Easdale & Healey, 2009; Wright et al., 2010). Most published growth–trait relationships are based on species-mean values and across-site comparisons, but it is expected that growth–trait relationships at the individual level and within sites are similar (Paine et al., 2015; Liu et al., 2016; Poorter, Castilho, Schietti, Oliveira & Costa, 2018). The difference between species and individual growth–trait relationships is that relationships at the species level represent potential growth–trait relations expected for the average individual of a species, while each particular relationship at the individual level represents a realized growth–trait relation (Poorter, Castilho, Schietti, Oliveira & Costa, 2018). These realized growth–trait relationships can be influenced by ontogenic stages, genetic differences between individuals within species or, in the present context, by the particular environment. Under similar abiotic conditions, the particular environment varies with regard to forest structure and will influence interactions among neighbour individuals (Kunstler et al., 2012; Fichtner et al., 2017, 2018). Due to the expected ontogenetic-stage (i.e. tree-size) dependency and the neighbour dependency of trait effects on growth (Iida et al., 2014a; Gibert, Gray, Westoby, Wright & Falster, 2016; Visser et al., 2016; Falster, Duursma & Fitzjohn, 2018), it would be interesting to determine how the growth–trait relationships would change during the development of young forests,

going from small saplings that not interact to taller trees that interact more intensively. During forest development tree sizes will determine forest structure, which at the local individual scale can have strong consequences. Trees with conservative strategies that for example prefer more shaded conditions would benefit from shade-providing taller neighbour trees, while trees with acquisitive strategies would be negatively affected by tall neighbour trees (Fichtner et al., 2017). Overall, changes in forest structure influence local environmental and competitive conditions that can influence individual growth–trait relationships. Functional traits are also used to explain performance or productivity at the community level by calculating abundance-weighted community mean values, and various measures of functional-trait diversity. These so-called community-weighted mean values or short CWMs are expected to be suitable predictors of community performance under assumptions of the mass-ratio hypothesis (Grime, 1998), whereas functional diversity indices are expected to be predictors under the niche-complementarity hypothesis (Petchey & Gaston, 2002). Such community-level trait indices are therefore used to test for potential mechanisms that underlie positive biodiversity effects, albeit often with limited success only (Roscher et al., 2012; Finegan et al., 2015; Kröber et al., 2015; Chiang et al., 2016; Cadotte, 2017; Huang et al., 2018). However, trait-driven resource competition occurs at the individual level, which means that aggregating individual trait values across species and communities ignores potentially large intra-specific variation caused by small-scale differences in environmental conditions or genetic variation. Therefore, inherent intra-specific variation can mask the true role of functional traits for growth, tree–tree interactions and community performance (Clark et al., 2011; Yang, Cao & Swenson, 2018).

Although the role of functional traits for community productivity has been investigated intensively in plant biodiversity experiments, the precise role of functional traits on individual growth across species-richness levels remains unclear (Roscher et al., 2018a). To understand the effects of various traits on tree growth, we collected trait and growth data at the individual tree level for 31 species growing in plots of five different species-richness levels in the BEF-China forest biodiversity experiment (Bruelheide et al., 2014; Huang et al., 2018). Specifically, we tested (1) if individual trait values changed with species richness at plot and neighbourhood scales; (2) if tree growth was more affected by traits or by species richness and if there was a richness-dependent trait effect on growth; (3) if growth–trait relationships changed with time and if this change depended on species richness. We expected (1) that trait values could change with species richness due the potential modifications of environmental conditions; (2) that traits had a stronger effect on growth than richness and that trait effects were stronger in stands of higher species richness due to presumably increased interspecific competition for resources; (3) that growth–trait relations changed with forest development and its interaction with species richness because of potential diversity-dependent changes in forest structure (e.g. tree sizes) and related environmental conditions (e.g. light availability).

MATERIAL AND METHODS

Study site

The BEF-China experiment is located in Dexing county, Jiangxi Province (29° 08′ – 29° 11′ N, 117° 90′ – 117° 93′ E). This region has a typical subtropical climate with a mean annual temperature of 16.7° C and precipitation of 1821 mm. January is the coldest

month with 0.4°C and July the warmest month with 34.2°C on average. The natural vegetation is characterized by subtropical forest with a mixture of evergreen and deciduous species. The experiment contains two field sites, A and B, with a total of 566 plots. Each plot has a projected ground area of 666.7 m^2 (25.8 × 25.8 m, equivalent to 1 mu, which is the traditional Chinese area unit). In each plot, 20 x 20 tree individuals were planted in 2009 (Site A) and 2010 (Site B), following a square grid design with an inter-tree horizontal distance of 1.29 m. Different tree species-richness levels (1, 2, 4, 8, 16 and 24 species per plot) were created with various species compositions along richness gradients that follow a so-called broken-stick design (Bruelheide et al., 2014; Huang et al., 2018). In this study, we use data from individual trees from plots with richness ranging from 1 to 16. The corresponding species occurred at every richness level.

Functional traits

Functional traits were collected at the end of the growing season from September to October in 2014 and 2015 in 59 plots from both sites. Originally, we planned to sample traits from four individual trees per species per richness level; however, due to logistical constrains (e.g. tree mortality in some plots) the final sample included 529 trees from 31 species (see Table S1 for species names and number of individual trees per richness level per species). On each tree we scored the number of first-order branches (first branching from the main axis, BrNr) and measured wood density (WD), leaf area (LA), specific leaf area (SLA), leaf chlorophyll content per area (CHL) and leaf nitrogen (LN), leaf phosphorus (LP) and leaf carbon content (LC) per unit mass. For a selection of 369 trees we additionally measured stomatal density (SD) and stomatal aperture (SA). For 288 trees

177 from Site A we measured specific root length (SRL) and root diameter (RD) for five orders
178 of roots. Due to high correlations between the five root orders, only values from the first
179 order (finest roots) were used in further analyses. WD (g/cm3) was estimated on three to
180 five segments from a total of three separate branches from the main stem for each tree, as
181 branch-wood density is a strong predictor of main stem-wood density (Swenson & Enquist,
182 2008). WD was calculated per branch segment by dividing the oven dried (80°C, 48 h) dry
183 weight with the water-displaced fresh volume. Five leaves were sampled per tree, weighed
184 for fresh weight, scanned for area (LA in cm^2) and dried for 48 h at 70 ˚C for dry weight,
185 after which SLA (cm2/g) was calculated. Chlorophyll content per area was estimated based
186 on measurements with a SPAD meter (SPAD-502, Minolta Camera, Japan). LN, LP and
187 LC (g/kg) were determined using the Kjeldahl method (Kjeltec 2200, FOSS, Höganäs,
188 Sweden) and a Mo Sb colorimetric method (UV-2550 Spectrophotometer; Shimadzu,
189 Kyoto, Japan). For three additional leaves, three stomatal imprints per leaf were made and
190 analyzed under a microscope (Nikon 80i). Stomata were counted for SD (count/mm^2) and
191 inner stomatal length and width were measured to calculate SA (μm^2) based on an elliptical
192 shape. All leaves used for trait measurements were fresh and healthy without any dirt,
193 physical damage or fungal infections. Roots were identified by tracking lateral roots of
194 target trees through the surface soil (depth 0~15 cm). The root systems were carefully
195 cleaned and dissected according to branching order. Order-specific roots were scanned and
196 analyzed with WinRHIZO (Regent Software, Canada) to measure root length and width
197 (root diameter). After scanning, the roots were dried for 48 h at 60°C. SRL (m/g) was
198 calculated as ratio of fresh root length to dry mass.
199

Growth rates

Growth rates were calculated as the absolute difference in stem basal area (cm^2) between years. Between 2013 and 2018, stem diameter 5 cm above ground level was repeatedly measured every year with a calliper at the same position that was permanently marked on the stem with white paint. Growth data were not available for all individual-by-year combinations of the 529 trees. The annual average growth rate (cm^2 $year^1$) for a 5-years interval was calculated on 404 individuals that had basal area data of 2013 and 2018. Yearly specific annual growth rates were calculated for 217 individuals that had basal area data for all the years between 2013 and 2018. We used absolute growth rates because we believe that these capture the biological consequences of plant growth and directly relate to the actual ecosystem function of forest growth and potential carbon accumulation (see Stoll et al., 1994; Liu et al., 2016). In addition, because we tested for growth–trait changes over years, we wanted to include the possibility of assessing changes in absolute growth rate due to increasing tree size (Iida et al., 2014a; Gibert et al., 2016).

Data analysis

First, one-way ANOVA and linear regression were used to assess if trait values changed with richness level and if a possible change was linear with each doubling of species richness (therefore, both plot and neighbour richness were log2-transformed). Plot richness was the total number of species planted per plot (containing 1, 2, 4, 8 or 16 species per plot). Neighbourhood richness was the number of different species represented by the survivors of the eight trees planted around the focal tree according to the rectangular planting pattern (containing 1 up to 8 neighbour species). These two richness measures

were used to distinguish between local community effects and local neighbourhood effects, respectively. In addition, multiple linear regression was used to estimate if trait-value changes with richness level differed between evergreen and deciduous species or between species in general or within the two groups.

Second, to determine the effects of functional traits on individual tree growth and to test if trait effects on growth were richness-dependent, data were analyzed with linear mixed-effects models using the 'lmer' function in the "*lme4*" package (Bates, Mächler, Bolker & Walker, 2015) of the R statistical software (R Core Team 2016). Annual growth for a five-year interval was the response variable. Trait values were first log or square-root transformed to increase normality and then z-transformed (mean = 0 and SD = 1) to foster comparability of effect sizes. Then, each trait was analyzed individually, i.e. ignoring effects of any other traits (Schmid, Baruffol, Wang & Niklaus, 2017). Plot richness and neighbourhood richness were analyzed separately to test if the local neighbourhood would have a different effect from the local community effect. Per analysis, richness was the first fixed-effects term (log2-transformed), followed by the trait and its interaction with richness (in this sequential order, type-I sum of squares for fixed effects). Site, plot and species identity were included as random-effects terms. This means that plot richness was tested at the level of plots, which were nested within plot richness, and any contrasts between groups of species could be tested against species identity, which was nested within potential species groups. By testing the effect of richness and trait sequentially we tested for a richness effect that could still be confounded to some extent by the trait, while fitting trait after richness tested the effect of trait values on growth nested within richness or, in other words, "while holding richness constant" (Schmid, Baruffol, Wang & Niklaus, 2017).

Analyzing the richness × trait interaction at the end tested if additional growth variation could be explained by the effect of richness-specific trait variation, in other words, different trait effects at different richness levels. Richness was analyzed log2-tranformed because this often linearizes relationships (i.e. constant changes in dependent variables for each doubling of species richness) and because it corresponds to the design of the diversity experiment that follows a log2-series (species richness 1, 2, 4 etc.). To determine the contributions of individual terms to the cumulative multiple R^2 of a linear model, we fitted all explanatory terms as fixed-effects terms in the following sequence: site (A vs. B), richness (log2-transformed), trait (z-transformed continuous values), richness × trait, species identity (31 levels) and plot (59 levels).

Third, to analyze the richness × trait interaction in more detail, i.e. to determine how the effects of multiple leaf traits on growth changed in a richness-dependent manner, stepwise linear regression analysis using all eight leaf traits was applied separately at each plot-richness level using the 'forward.sel' function of the "*packfor*" package in R (Dray, Legendre & Blanchet, 2017).

Fourth, to test the summarized effect of leaf traits on growth, we also calculated the first two principle components of the eight standardized traits (PC1 and PC2; 'rda' function of the "*vegan*" package in R; Oksanen et al., 2016) and analyzed their effects on growth for the different richness levels. Individuals were categorized as acquisitive or conservative by separating the individuals in two equally sized groups based on their PC1 value (separating at median). Categorizing individuals in acquisitive and conservative did not result in equal distinction as categorizing deciduous and evergreen; of the 142 deciduous individuals 52 were conservative while of the 151 evergreen individuals 59 were

categorized acquisitive. At last, to estimate if the effects of trait values on growth changed over time, linear regressions were used to test the effects of each trait on yearly growth rates per plot-richness level separately.

RESULTS

Trait changes with species richness

Leaf phosphorus (LP), leaf chlorophyll (CHL) and number of branches (BrNr) were the only traits that significantly changed with plot species richness across all species (Fig. 1 and Table S2), although R^2 was relatively low. LP decreased, while CHL and BrNr increased with increasing plot richness (Fig. 1). The increase of BrNr with plot richness was mainly caused by the 16-species mixture, indicated by the significant differences between 16-species and 1, 2 and 4-species mixtures (Fig. 1c). Specific root length (SRL) and root diameter (RD) also differed between specific richness levels: the 2-species and 4-species mixtures where different from the other plot richness levels (Fig. S1). Trait-value changes with richness level were similar for evergreen and deciduous species (except for CHL and RD), while almost all traits expressed significant species-dependent trait changes in response to plot richness (Table S3). Nonetheless, if species were analyzed separately (with lower statistical power due to smaller number of replicates), only for a few of them did trait values change significantly positively or negatively with plot richness (Fig. S2). In contrast to the response to plot richness, individual trait values showed no significant linear change across the logarithm of neighbourhood richness. However, LA, LN, LC and RD showed some differences between richness levels (indicated by the ANOVA results

where neighbourhood richness was fitted as 5-level factor), which were not accounted for by the log-linear contrast for neighbourhood richness (Table S2).

Effects of traits on individual-level tree growth

Annual growth of individual trees over the 5-year interval was not affected by plot or neighbour richness but was significantly affected by five traits: LA, LN, LC, CHL and BrNr (Table 1 for plot and Table S4 for neighbour richness). In addition, the interaction between richness and trait was significant for LA, SLA, LC, SD, SRL and BrNr, indicating that richness-dependent trait effects on growth were relevant despite the large variation in tree growth related to species and plot identity (on average 43 and 14 % respectively, Fig. S3). LA and SLA had a positive effect on growth at high species richness while this relationship was weakly negative at low richness (Fig. 2a-b). LC, SD and SRL had a negative effect at high while having no or slightly positive effects at low richness (Fig. 2c-e). BrNr had a positive effect at both low and high richness, but the effect increased with increasing richness (Fig. 2f). Overall the traits had stronger effects on individual tree growth at higher than at lower richness levels. The major axis of the principal component (PC) analysis representing the eight leaf traits also indicated a richness-dependent effect on growth (Table S5, Fig. S4). We interpreted this first PC axis as a gradient from acquisitive to conservative leaf traits, which showed a strong negative relationship with growth at high richness levels. Categorizing the individuals into two equally sized groups of acquisitive vs. conservative strategy, based on their scores on the first PC axis, did indicate that the growth difference between acquisitive and conservative individuals increased from monocultures to higher species-richness levels (Fig. S4). Assessing which

of the traits explained most of the variation in growth, in a richness-dependent manner, resulted in different trait affecting growth most strongly at different levels of plot richness. For example, CHL was the most important trait in monocultures, while LA was most important trait in 16-species mixtures (Table S6).

Yearly changes of trait effects on individual-level tree growth

Separating total growth into yearly growth increments and analyzing growth–trait relationships per plot-richness level separately, likewise revealed significant growth–trait relationships, albeit fewer (but still many more than the 5% with $P<0.05$ expected by chance; Moran 2003) due to the smaller sample sizes and thus lower statistical power (Table S7). BrNr and CHL had the most significant relationships with individual tree growth across years and per richness level: out of a total of 25 regressions, 24 (BrNr) and 18 (CHL) were significant. The growth–trait relationships for these two traits changed slightly across years, and these changes were different at different richness levels. However, a consistently increasing or decreasing growth–trait relationship over time could not be identified. The positive relationship between BrNr and growth strengthened with time and was stronger at higher richness levels than in monocultures (Fig. 3 and Table S7), consistent with the overall finding reported above. Although the linear mixed-effects model did not indicate a significant interaction between CHL and richness on growth, the relationship of CHL with yearly growth was in general weak at higher plot richness levels while it was strong in monoculture (Fig. S5 and Table S7).

DISCUSSION

In our analysis we showed that the growth of individual trees in a forest biodiversity experiment was more affected by traits than by species richness, but that, at the same time, trait effects on growth increased with species richness. This indicates that the environment surrounding an individual tree shapes the roles that the traits of this individual have on growth. Elucidating how functional traits affect the growth of individual trees in a diversity-dependent manner is a necessary initial step to scale-up and analyze how trait variations are related to community performance via the cumulative effects on individual tree growth.

Trait–richness relationships

Across 31 species, three (LP, CHL, BrNr) out of twelve traits measured at the individual-tree level changed consistently with plot-species richness, while two additional traits (SRL, RD) showed differences between specific plot richness levels. We expected that traits would change in response to plot richness because variation in community-level species richness and species composition influences the local growing environment, which can affect the trait values of individuals (Roscher et al., 2011; Lipowsky et al., 2015). However, at the level of local neighbourhood richness no trait consistently changed with species richness. This might have been due to the fact the local neighbourhood richness was varying randomly within plot richness, which was the experimentally designed explanatory variable. The observation of a consistent increase of BrNr and CHL with the community-level plot richness could be related to increased light availability caused by light partitioning among individuals from different species at high levels of species richness (Stoll & Schmid, 1998; Sterck, 1999). The decrease of leaf phosphorus with plot richness

was not expected, but could be related to soil properties, just like the root-trait values at specific richness levels. Leaf phosphorus is highly related phosphorus availability in the soil, and if limited can reduce photosynthetic processes (Reich, Oleksyn & Wright, 2009). The sensitivity of SRL values to species richness was consistent with earlier findings of Bu et al. (2017) in the same experiment.

Trait responses to species richness differed among species, which weakened overall effects of species richness on trait responses across species. However, these differences among species were not related to differences between deciduous and evergreen species. These results suggest that traits of young trees have species-specific sensitivities to species richness, as has previously been observed for herbaceous plant species in grassland biodiversity experiments (Gubsch et al., 2011; Roscher et al., 2011; Lipowsky et al., 2015).

At community level, trait changes caused by species richness can affect species performance and community productivity, as demonstrated for various ecosystems including grasslands (Zuppinger-Dingley et al., 2014), crop fields (Zhu, van der Werf, Anten, Vos & Evers, 2015) and forests (Jucker, Bouriaud & Coomes, 2015). Even though these studies showed that trait plasticity in response to species richness can be common, to our knowledge only one study considered diversity-specific trait values to calculate realized community-level indices (such as community-weighted means or functional diversity) to determine the role of functional traits on community productivity (Roscher et al., 2018b). As the origin of the trait values can influence the ability of community indices to explain biodiversity effects (Roscher et al., 2018b), future BEF research should consider functional trait variation induced by diversity also in forest ecosystems, as our results suggest.

383

384 **Growth–trait relationships across richness levels**

385 Even though we could not detect significant effects of species richness on individual-tree
386 growth directly, richness still significantly affected tree growth by changing growth–trait
387 relationships. While some traits — LN and CHL — showed consistent growth–
388 relationships across richness levels, other traits — LA, SLA, LC, SD, SRL and BrNr —
389 showed a richness-dependent relationship. Overall these growth–trait relationships were
390 stronger at higher than at lower richness levels (Fig. 2). That trait values and the trait ×
391 richness interaction explained a significant variation in individual-tree growth in the face
392 of large variation among the 31 different tree species suggests that in general, among all
393 species, the relationships between traits and growth are ecologically relevant.
394 Understanding the role of traits on growth beyond species identity will increase the
395 understanding of general characteristics of trees for growth across gradients of species
396 richness. The observations that the relationship between growth and the first PC axis
397 changed with increasing richness, and that individuals categorized as acquisitive (higher
398 LA, SLA and LP) versus conservative had increased growth differences with increasing
399 species-richness levels, suggested that effects of tree characteristics on growth depended
400 on the local and community-level biotic environment of individual trees.

401 Although all species occurred at all richness levels, in monocultures competition
402 was only intra-specific while in species mixtures there was considerable inter-specific
403 competition, increasing with species richness. This means that competition occurred
404 probably between individuals with more similar trait values in monocultures, while
405 individuals with more different trait values competed in species mixtures. Likely, this

406 difference in competition affected individual growth, as also indicated by previous studies
407 illustrating that the effect of trait values on growth depends on the trait values of the
408 neighbours (Uriarte et al., 2004; Kunstler et al., 2012). Additional speculations on possible
409 mechanisms behind this observation, which to our knowledge has not previously been
410 reported in the BEF literature, are difficult. Nevertheless, our findings suggest that growth–
411 trait relationships in tree monocultures may not be predictive of growth–trait relationships
412 in mixtures, possibly explaining why previous attempts to use species-level trait values to
413 analyze individual and community growth in mixtures had limited success (Liu et al., 2016;
414 Yang, Cao & Swenson, 2018). Diversity-dependent trait effects on tree growth may be
415 expected at the individual-tree level because individual-tree growth depends on neighbour-
416 tree interactions such as competition and facilitation. Differences and hierarchies between
417 functional traits of neighbour trees influence competition and facilitation, by which the role
418 of the focal trait on growth can depend on trait values, growth strategy and size of
419 neighbours (Uriarte et al., 2004; Kunstler et al., 2012; Fichtner et al., 2017, 2018).
420
421 **Yearly changes in growth–trait relationships**
422 Growth–trait relationships in consecutive yearly intervals were significant only for BrNr
423 and CHL across plot species richness levels. Due to the absence of growth–trait relations
424 per year for the other traits we cannot conclude if growth–trait relationships became
425 stronger over time related to tree age and forest development. Growth–trait relationships
426 in young trees were expected to change with time due to size-dependency of trait effects
427 on growth and due to changes in forest structure (Iida et al., 2014b; Gibert et al., 2016;
428 Visser et al., 2016). Over the years, especially in more species-rich communities, size

differences become more apparent due to asymmetric light competition (Weiner 1990) by which individual trees can adjust to the appropriate conditions by trait plasticity related to acquisitive or conservative strategies. This suggests that the observed richness-dependent trait effects on growth that could be related to the increased growth difference between acquisitive and conservative individuals in species-rich plots, would become more apparent over time. The data did show that yearly specific growth–trait relations at the individual level were difficult to capture, although in theory traits are expected to affect individual growth through trait differences among neighbouring trees. Here, the scale of our study was a limiting factor, because replication was low, such that overall effects like differential responses of species to richness were significant even though most individually-tested responses were not. Future studies with higher replication and longer time-spans for growth measurements could disentangle how growth–trait relationships change during tree and forest development in more detail. More knowledge about trait effects on growth in diverse systems will enable us to enhance tree-growth models that are used to predict tree and forest growth responses to changing environments.

The role of diversity-dependent individual growth–trait relationships for positive community-level biodiversity effects

Of the eight traits that significantly influenced growth, six showed a richness-dependent effect on growth. The observed growth differences that were linked with trait differences were stronger in high- than in low-diversity communities. While diversity effects are often suggested to be mediated by traits, we showed that diversity also has an effect on growth by influencing the effect of traits on growth. This novel observation illustrates that small-

scale environmental differences created by species richness and composition influence individual tree growth. In addition, local species identity and diversity can produce similar effects, for example via neighbour size and neighbour traits (Kunstler et al., 2012; Liu et al., 2016; Fichtner et al., 2017, 2018; Roscher et al., 2018a). That the diversity dependencies of traits may have translated into an increasing growth difference between acquisitive and conservative strategies with increasing species richness is not surprising in young forests. During early forest development, fast-growing individuals (acquisitive strategies) might benefit asymmetrically by light competition (Weiner 1990) in mixtures, suppressing slow growing individuals, a scenario that could not occur in monocultures. However, we expect that growth–trait relationships in mixtures change again in older forests, because conservative individuals should be better adapted to the shaded environment created by the fast-growing individuals, thus possibly catching up in growth via different growth–trait relationships (Holzwarth, Ruger & Wirth 2015).

Understanding how growth–trait relationships at the individual level change with species richness and time is a prerequisite to understanding biodiversity effects at community level. However, at the same time there may be additional effects of traits and diversity-dependent trait variation on growth, which will not be reflected directly in biodiversity effects, as shown in the present study. Although strong overall effects of plot (community-level) or neighbourhood (local) richness on individual-tree growth were absent, within a given richness level trait variation and richness-dependent trait variation had clear effects on individual-tree growth. Overall, the observation that species richness as biotic environment influences growth–trait relationships of individual trees emphasizes that extrapolation from species-level relationships, in particular those observed in

475 monoculture plantation, will not allow us to delve into mechanisms underlying effects of
476 plant species richness on community performance.
477
478 **CONCLUSIONS**
479 In this study we assessed how growth–trait relationships at the individual-tree level
480 depended on species richness at community and local neighbour scale. Using a planted
481 forest biodiversity experiment, we found that trait effects on growth were stronger at higher
482 levels of plot richness creating a larger difference between acquisitive and conservative
483 growth strategies at higher than at lower richness or in monocultures. The observed
484 diversity-dependent trait effects on growth are consistent with other studies showing that
485 plant growth depends on local conditions created by neighbour identity, size or traits.
486 Knowing how functional traits affect growth in a diversity-dependent manner gives insight
487 in how individual-level trait variations may scale up to community performance through
488 the cumulative effects of the performance of individual trees.
489
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AUTHOR'S CONTRIBUTIONS

XL and KM designed the experiment, ZS, SL, YL, WH, GvO, YL and SL conducted the measurements and FJB and XL performed data analysis. MS and BS helped designing the project and analyzing the data. FJB and XL, with the help of BS, wrote the paper. All authors contributed to the final preparation of the manuscript.

DATA ACCESSIBILITY

All data will be available on the BEF-China project database at http://china.befdata.biow.uni-leipzig.de/datasets.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

TABLE S1. Number of individual trees per species per richness level for which trait values were measured.

TABLE S2. Results of linear regression analyses and one-way ANOVA of individual trait values and plot richness and neighbour richness.

TABLE S3. Results of multiple linear regression analyses of individual trait values related to plot richness (PR), deciduous or evergreen species (DE), species identity (Species) and the interactions.

TABLE S4. Summary of linear mixed-effects models for effects of neighbour species richness, traits and their interaction on annual growth over a 5-year period at the individual-tree level.

TABLE S5. Summary of linear mixed-effects models for effects of plot or neighbour richness (PR and NR, respectively) and PC1 and PCP2 and their interactions on growth.

TABLE S6. Results of the forward stepwise multivariate regression analysis of leaf traits affecting growth.

TABLE S7. Slope and R2 values with related significance (between brackets) of linear regression analyses of individual traits and year-specific basal area growth (log) separatly per plot richness level.

FIGURE S1. Trait values of specific root length (SRL, a) and root diameter (RD, b) per plot richness.

FIGURE S2. Visualization of species-specific regressions of trait values with increasing plot richness.

FIGURE S3. Percentage explained variance of individual basal area growth over a 5-year period for all factors considered in the study.

FIGURE S4. Illustration of the principal component analysis, the plot richness-dependent relationship of the first PC axis (PC1) and basal-area growth and the categorization of acquisitive and conservative individuals with their richness-dependent growth.

FIGURE S5. Effect of leaf chlorophyll on five consecutive year-specific annual basal-area growth rates at five plot species-richness levels.

TABLES

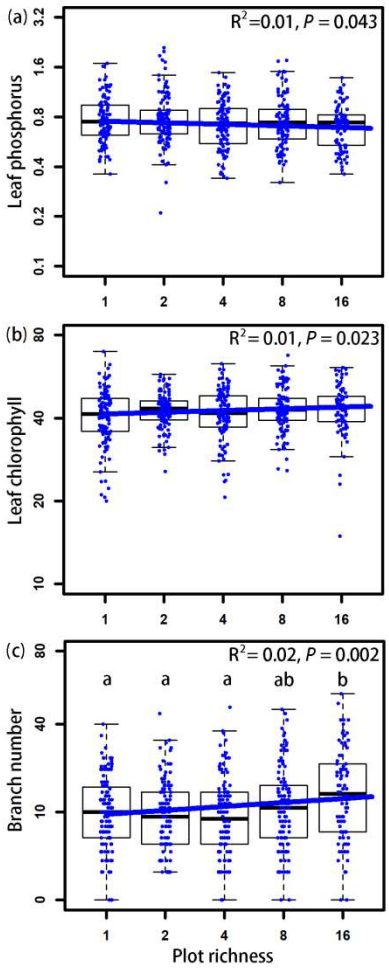
TABLE 1. Summary of linear mixed-effects models for effects of plot species richness, traits and their interaction on annual growth over a 5-year period at the individual-tree level. Growth data represent the average absolute increase of basal area between 2013 and 2018 divided by five. Trait values were standardized after log or square-root transformation. Denominator degrees of freedom (dDF), *F*-values and *P*-values are based on sequential fits of fixed effects (corresponding to type-I sum of squares analysis).

	LA (n=400)			**SLA (n=400)**			**LN (n=400)**			**LC (n=400)**		
Source of variation	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*
log2(PR)	11.51	0.97	0.346	9.82	0.85	0.378	13.17	0.85	0.372	16.10	0.75	0.398
TRAIT	290.14	9.78	**0.002**	296.84	0.00	0.992	286.42	4.75	**0.030**	384.21	4.81	**0.029**
log2(PR)×TRAIT	130.08	20.88	**<0.001**	130.43	8.47	**0.004**	169.50	2.60	0.109	264.72	6.47	**0.012**
	LP (n=400)			**CHL (N=403)**			**SA (n=297)**			**SD (n=301)**		
Source of variation	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*
log2(PR)	13.90	0.85	0.371	13.53	0.91	0.357	6.47	0.01	0.932	8.50	0.00	0.996
TRAIT	283.79	0.68	0.410	392.14	18.97	**<0.001**	259.47	3.73	0.055	149.48	0.46	0.498
log2(PR)×TRAIT	207.35	0.02	0.878	284.60	0.42	0.517	91.58	3.13	0.080	103.48	8.48	**0.004**

Source of variation	SRL (n=209)			RD (n=209)			WD (n=388)			BrNr (n=402)		
	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*	dDF	*F*	*P*
log2(PR)	9.42	3.53	0.091	6.90	3.14	0.120	14.67	0.10	0.759	18.65	0.46	0.506
TRAIT	159.82	1.50	0.223	115.44	0.83	0.364	349.31	0.89	0.345	341.15	272.74	**<0.001**
log2(PR)×TRAIT	114.27	4.56	**0.035**	175.64	2.92	0.089	208.17	1.08	0.300	348.44	4.70	**0.031**

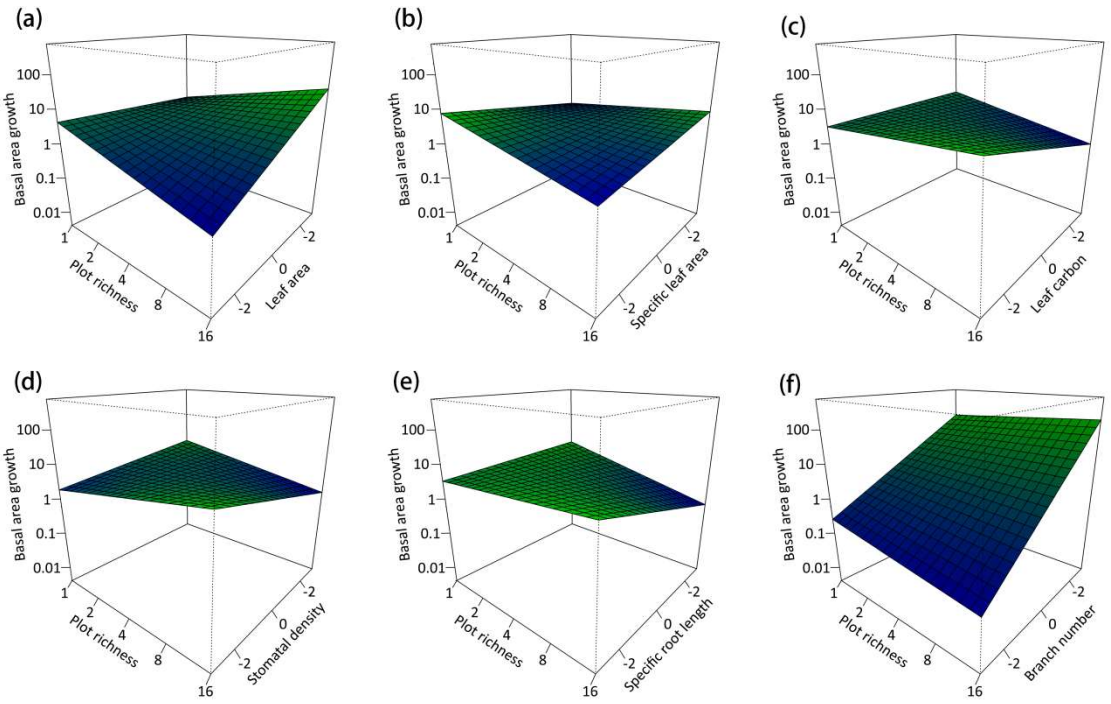
**Mixed-effects models were fitted with site, species composition and species identity as random effects. Site was not included as random effect for root traits because root samples were only taken in site A. All degrees of freedom have been calculated with Satterthwaite approximation. All fixed terms were fitted sequentially (corresponding to type-I sum of squares). PR: plot richness; LA: leaf area; SLA: specific leaf area; LN: leaf nitrogen LC: leaf carbon; LP: leaf phosphorus; CHL: leaf chlorophyll; SA: stomatal aperture; SD: stomatal density; SRL: specific root length; RD: root diameter; WD: wood density; BrNr: number of branches. Bold numbers are significant at P<0.05.*

735 **FIGURES**



736

737 **FIGURE 1.** Linear regressions between plot richness and the traits (a) leaf phosphorus
738 (LP), (b) leaf chlorophyll (CHL) and (c) branch number (BrNr). For visualization purposes,
739 data points are slightly jittered per plot-richness level and boxplots illustrate median with
740 upper and lower quartile and whiskers at quartile ±1.5 × interquartile range. Letters in panel
741 (c) represent the differences between the richness levels based on the one-way ANOVA
742 using species richness as 5-level explanatory factor rather than log-linear richness. The x-
743 axes are log2-transformed and the y-axes are log-transformed for leaf phosphorus and
744 chlorophyll and square root-transformed for branch number. See Table S2 for summary
745 statistics.



746

747 **FIGURE 2.** Visualization of model predictions of plot richness-dependent growth–trait
748 relationships (Table 1) for (a) leaf area (LA), (b) specific leaf area (SLA), (c) leaf carbon
749 (LC), (d) stomatal density (SD), (e) specific root length (SRL) and (f) branch number
750 (BrNr). Model predictions are based on linear mixed-effects models including plot richness
751 (log2-transformed), trait (z-transformed values: mean = 0, SD = 1) and their interaction as
752 fixed-terms and site, plot and species identity as random terms (site was not included for
753 specific root length). Growth is the annual growth of the 5-year interval between 2013 and
754 2018 on a log-scale. Colours represent low (dark blue) to high (bright green) growth.

755

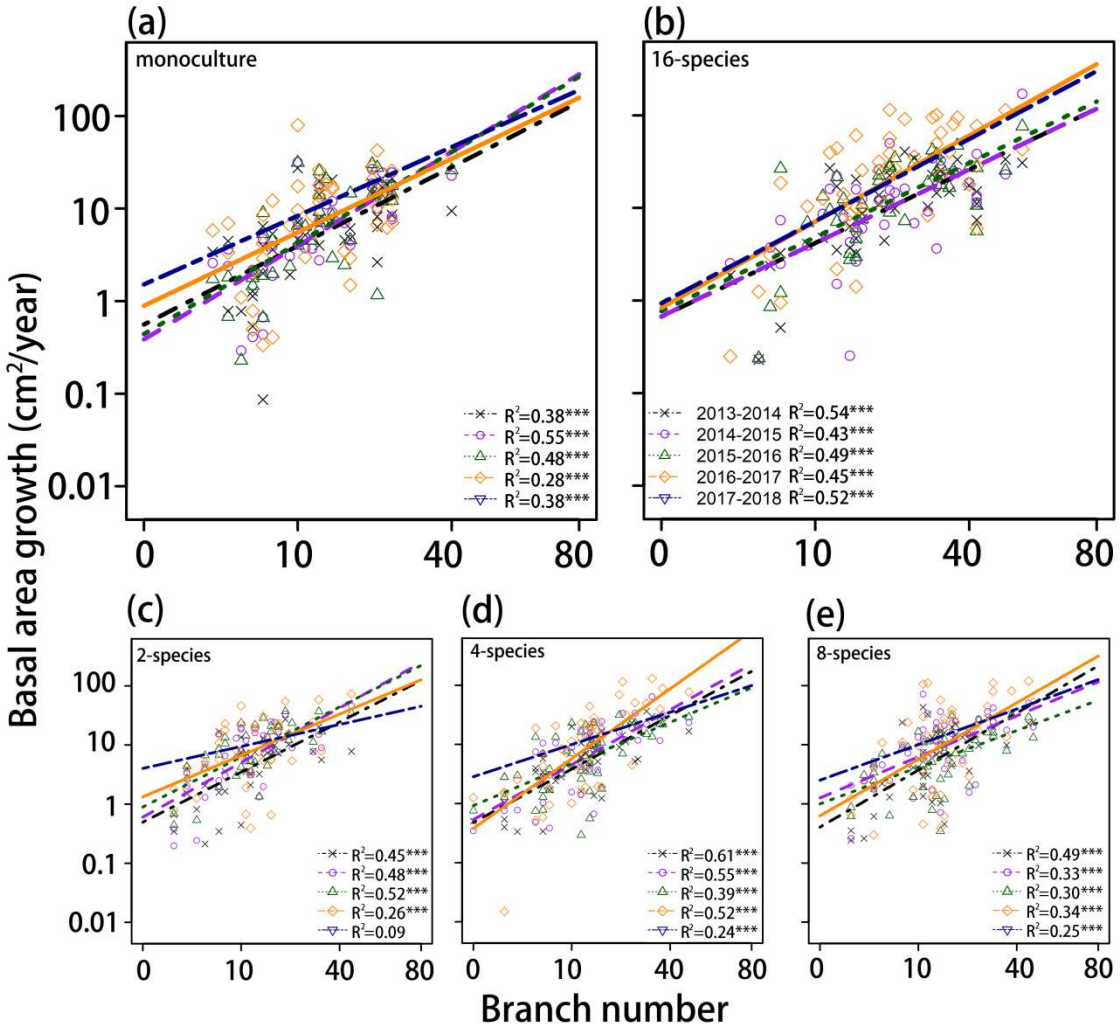


FIGURE 3. Effect of branch number on five consecutive year-specific annual basal area growth rates at five plot species-richness levels. Different lines represent regressions between number of branches and growth for the different years. Per year R^2 and significance are presented in in-figure legends and year-specific slopes are presented in Table S8. * $P<0.05$, ** $P<0.01$, *** $P<0.001$.